Survival Probability of Adult
Yellow Warblers in Montana

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# Survival Probability of Adult Yellow Warblers in Montana: Effects of Dispersal and Model Types

**FINAL REPORT**

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## ABSTRACT

Survival probability estimates for songbirds are generally conservative because dispersal between breeding seasons is not differentiated from mortality. Presently, knowledge of between-year breeding dispersal is lacking for most songbirds. To assess survival probabilities and dispersal, 436 adult Yellow Warblers (*Dendroica petechia*) were color-banded and resighted over five breeding seasons at 11 study sites in the Bitterroot Valley, Montana. During the last two seasons, we searched extensively for marked warblers between and surrounding these sites in order to compare survival probabilities with and without this added dispersal information and to assess the effectiveness of adjusting survival probabilities with transient models. Survival probabilities were calculated using open population models, and model selection was based on Akaike's Information Criterion (AIC) within program MARK. The best model indicated that survival probabilities differed between males and females and varied among years. We found that dispersal off the original study site was more common than anticipated (30% dispersal in 1999), and survival probabilities increased by 6.5-22.9% with the inclusion of dispersed birds. Overall transient models appeared ineffective at distinguishing permanent emigrants from mortalities. We suggest emigration can have substantial effects on survival probabilities, and advise against the use of return rates from small study areas. In addition, our results suggest that transient models may not reliably increase the accuracy of survival probability estimates.

Keywords: apparent survival probability, breeding dispersal, transient models, mortality, Yellow Warbler, *Dendroica petechia*

## INTRODUCTION

Loss, alteration, and fragmentation of songbird breeding habitat may cause changes in population status (Terborgh 1989, Hagen and Johnston 1992, Donovan et al. 1995a, 1995b, Faaborg et al. 1995, Freemark et al. 1995). Population status is commonly assessed by monitoring trends in abundance over time through programs such as the Breeding Bird Survey (Sauer et al. 1999). Presently, analyses of trend data are disputable, at times contradictory (e.g. Bohning-Gaese et al.1993, James et al. 1996, Sauer et al. 1996) and cannot inform us of the reasons for population changes (Van Horn 1983, James and McCulloch 1995, Thompson et al. 1998, Nichols 1999). Accurate estimates of demographic parameters are necessary to understand songbird population dynamics and the underlying mechanisms causing population changes (Temple and Wiens 1989, Brawn and Robinson 1996, Loery et al. 1997). Knowledge of demographic parameters may also clarify discrepancies in population trend analyses (Brawn and Robinson 1996).

The demographic parameters responsible for changes in population sizes are seasonal fecundity, survival probability, and dispersal probability (emigration and immigration) (Temple and Wiens 1989, Hestbeck et al. 1991, Brownie et al. 1993, Loery et al. 1997, Koenig et al. 2000). Seasonal fecundity in birds is estimated by combining data from nest monitoring studies with seasonal productivity models (Donavon et al. 1995b, Pease and Gryzbowski 1995). Adult survival probability is commonly estimated from recapturing or resighting marked individuals over multiple years at one or more study sites. Direct estimates of juvenile survival probability are not generally available because juveniles commonly disperse from natal areas (Greenwood and Harvey 1982). These estimates have often been obtained by dividing adult mortality by mean number of young fledged (Ricklefs 1973, Anders et al. 1997), resulting in rates ½ to ¾ of adult

survival (Greenberg 1980, Temple and Carey 1988, Thompson 1993, Donovan et al. 1995b, Brawn and Robinson 1996). Arguably, the least known and most often ignored parameter is dispersal (Rockwell and Barrowclough 1987, Brawn and Robinson 1996; Koenig et al. 2000; Walters 2000). Because natal and breeding dispersal are difficult to observe, permanent emigration and mortality are not distinguished in estimates of passerine survival (Zeng and Brown 1987, Payne and Payne 1990, Peach 1993, Johnston et al. 1997).

Although avian adult survival probability is a commonly reported and critical demographic parameter, its use and definition are inconsistent. *True annual survival probability* ($s$), often the parameter of interest, is defined as the probability that an individual alive at time $t$ survives to time $t + 1$. This parameter is generally estimated with band recovery models (Brownie et al. 1985) and, in some cases, with multistate models (Brownie et al. 1993, Nichols and Kaiser 1999). *Apparent survival probability* ($\phi$) is defined as the probability that an individual alive at time $t$ survives to time $t + 1$ and does not permanently emigrate from the study area between time $t$ and $t + 1$. Apparent survival probability is usually estimated with open population models (Lebreton et al. 1992), and in these models, true survival and emigration probabilities are confounded, but the detection probability ($p$; the probability of detection, given a bird is alive and in the population associated with the study area) is estimated separately. *Return rates* are the product of apparent survival probability and detection probability (Martin et al. 1995, Lindberg et al. 1998, Anderson et al. *in press*). True survival, permanent emigration and capture probabilities are all confounded in this metric, yet many bird studies erroneously report the *return rate*, as an estimate of *apparent survival probability* or *true survival probability* (Lebreton et al. 1993; Martin et al. 1995).

Estimates of true survival probability are likely not obtainable for small passerines without additional advances in radio marking technology (or the initiation of a hunting season on songbirds). Therefore, assessments of the extent that permanent emigration affects estimates of apparent survival probability are needed. These assessments require data on the movements of birds between breeding seasons. Dispersal off the study site is generally not considered in the demographic breeding bird studies from relatively small, single study areas, though some have proposed mathematical adjustments to correct for bias in dispersal distance due to finite study areas (Cunningham 1986, Barrowclough 1987, Zeng and Brown 1987, Baker et al. 1995). However, to our knowledge, there have been few songbird mark-resight studies with the objective of resighting individuals outside the boundaries of the original study area (but see Tiainan 1983, Beletsky and Orians 1987, Jakobsson 1988, Wheelwright and Mauck 1998, Woodworth et al. 1998), and none with the goal of using this information to refine estimates of adult survival probability.

An alternative approach for adjusting estimates of apparent survival probability for permanent emigration is transient modeling (DeSante et al. 1995, Pradel et al. 1997, Loery et al. 1997). These models attempt to identify and exclude transients (individuals that are thought to be permanent emigrants) from estimates of survival probability. However, heterogeneity in survival probability and capture probability may over-inflate estimates of $\phi$ in these models. Individuals that are excluded because they are believed to be transients may simply be mortalities or individuals with low capture probabilities.

A paucity of avian dispersal information coupled with evidence of between-year movements within a population of Yellow Warblers (*Dendroica petechia*) led to this study. Our primary objectives were to 1) refine apparent survival estimates using knowledge of between-year breeding dispersal; 2) determine the value of altering the sampling design to include extended searches for marked individuals surrounding the study sites; and 3) assess the effectiveness of transient models to reduce the effects of permanent emigration on estimates of songbird survival probability.

## STUDY AREA AND METHODS

We established seven study sites on a combination of pubic and private lands along the Bitterroot River in western Montana and four smaller sites along riparian drainages within the western foothills, primarily in the Bitterroot National Forest (Fig.1). These core sites averaged 15 ha in size (range 5-20 ha) with elevations of 1050-1350 m. All sites were deciduous riparian habitats. The Bitterroot River sites were dominated by deciduous trees and shrubs, especially black cottonwood (*Populus trichocarpa*) and were surrounded by residential areas, agricultural lands (cultivated and/or grazed by cattle or horses), and deciduous and coniferous forest communities. The foothill sites were dominated by shrubs and deciduous trees, especially quaking aspen (*Populus tremuloides*), and were surrounded by coniferous forests and some grazed lands. Study sites were initially chosen to minimize differences in habitat character among sites, although there was a range in landscape variation surrounding the sites (see Tewksbury et al. 1998).

During the breeding season, Yellow Warblers are the most common species of deciduous riparian areas within the Rocky Mountain West (Tewksbury et al. *in press*). In western Montana, they arrive on the breeding grounds and begin to establish territories during the last two weeks of May, with males generally arriving 2-7 days before females (Tewksbury and Cilimburg *unpublished data*). They are found in association with streamside shrubs or large deciduous trees, especially black cottonwood, and may also be found within the deciduous vegetation of residential areas (Hutto and Young 1999; Cilimburg *unpublished data*).

During the 1995-1998 breeding seasons (approximately 23 May – 1 August), we created territory maps of breeding Yellow Warblers on the 11 core sites and target mist-netted adults, often with the help of playback songs and calls. Both females and males respond to playback songs or calls, though females less so, especially during incubation. We aged and sexed by plumage all captured birds, and we marked individuals with one US Fish and Wildlife Service metal band and a unique combination of three color bands. As this was part of a larger study (Tewksbury et al. 1998, Tewksbury 1999), field assistants searched for and monitored nests, mist netted, or resighted marked individuals at each core site every one to three days throughout the season. The perimeters of each site (approximately 100-200 m depending on available habitat) were searched for banded birds in 1996 and 1997.

During the 1998 and 1999 seasons we expanded our resighting area and searched for banded individuals within suitable habitat along the Bitterroot River between and surrounding the core sites (Fig. 1). We concentrated our efforts around the sites where the most birds were banded (sites #1, 2, 3, 4, 6). We surveyed about 85-90% of available Yellow Warbler habitat between sites #1-3 during each of these two seasons; surveys around the other sites were less complete (see Fig. 1). For these searches, two field researchers systematically traveled sections of the

river corridor, sighted individuals and determined the presence or absence of bands and, when present, the color combination. We again used song playbacks to attract pairs and played songs in appropriate warbler habitat when there was no visible or audible activity. As males are commonly located first, we placed extra effort in sighting the female associated with each male. We approached sites by foot whenever possible and used kayaks to access small islands. Resighting time for the expanded dispersal searches totaled approximately 220 hours in 1998 and 380 hours in 1999 and generally occurred between 0600 and 1300 hours. In 1998, sampling occurred from 26 May – 8 July. In 1999, we divided the season in half, resighting from 27 May – 12 June and repeating the surveys 20 June – 12 July. We split the season to avoid confounding survival probabilities and detection probabilities in the fully time-dependent Cormack-Jolly-Seber models (Lebreton et al. 1992). This allowed time-specific parameter estimations to be assessed in 1999.

Territory centers were used to determine the distance moved between years. We used a *Trimble Geoexplorer* GPS unit to mark exact locations of banded individuals found off the core sites. In 1999, the territory centers for all banded individuals and the boundaries of all core sites were mapped via GPS. From the territory site maps, we digitized approximate territory centers for each bird in 1995-1998, and from these locations, computed straight-line dispersal distances using UTM coordinates.

*Data analysis – parameter estimation.* – We used Cormack-Jolly-Seber (CJS) models to estimate annual apparent survival probabilities ($\phi$) and detection probabilities ($p$) (Lebreton et al. 1992, Nichols 1996). The model set was determined a priori and was based on Yellow Warbler biology and the question of interest (Burnham and Anderson 1998, Anderson and Burnham 1999). For both $\phi$ and $p$, we assessed gender- and year-specificity and the interaction between these variables (Table 1A and B).

To assess how resighting in the expanded search areas affected estimates of apparent survival and detection, we ran two separate analyses. The data for the first analysis included all individuals banded and those resighted in subsequent years on the study site on which they were originally banded (hereafter termed "core analysis"). For the second analysis, we included core analysis data, banded birds sighted off the study sites (via the extended searches in 1998 and 1999), and sightings of individuals on a site other than their site of origin (hereafter termed "dispersal analysis").

We used program MARK (White and Burnham 1999) to generate maximum likelihood estimates of $\phi$ and P and relied on Akaike Information Criteria (AICc, adjusted for sample size) to determine the best approximating model among the suite of candidate models. This approach determines the model that best explains the data while incorporating the fewest parameters, thus balancing tradeoffs between sampling variance and bias (Burnham and Anderson 1998, Anderson and Burnham 1999). To test our assumptions of model fit (lack of independence among individuals, heterogeneity in $\phi$ and/or P), we ran bootstrap Goodness of Fit (GOF) tests (1000 replications) on the fully parameterized model for both sets of analyses (Lebreton et al. 1992, Burnham and Anderson 1998). From this analysis, we calculated ĉ, the measure of fit, defined as the global model deviance divided by the mean bootstrap deviance (White and Burnham 1999).

*Data analysis – transient models.* – Pradel et al. (1997) developed mark-recapture models that attempt to detect otherwise indistinguishable transients within a population in order to provide true survival estimates for residents. These models assume individuals resighted at least once are residents, and a high but unknown proportion of those initially marked and never resighted are transients. Transients are operationally defined as having an apparent survival probability of 0.00 (Loery et al. 1997, Pradel et al. 1997). According to Pradel et al. (1997), two modeling approaches can be used to detect transients, the ad hoc test and the Robson test. For the ad hoc test, parameters are estimated only for residents, those individuals recaptured or resighted at least once. With the Robson test, apparent survival probabilities and detection probabilities are estimated separately for those newly captured and those resighted at least once. The proportion of residents in the population is then estimated by dividing the survival probability of the newly marked individuals by the survival probability of the residents. Pradel et al. (1997) showed that the ad hoc test was a reasonable approximation of the Robson test when detection probabilities were high.

To assess the appropriateness of using transient models to clarify the proportion of residents and transients, we ran the ad hoc and Robson tests using the core analysis data set and compared these results to estimates obtained from the dispersal analysis. We used program MARK (White and Burnham 1999), altering the input file for the ad hoc test (suppressing the first capture within the capture history for each individual), and altering the parameter index matrix within MARK for the Robson test (Pradel et al. 1997). We report the survival probabilities and detection probabilities using the model structure from the previously determined best approximating model for the core analysis.
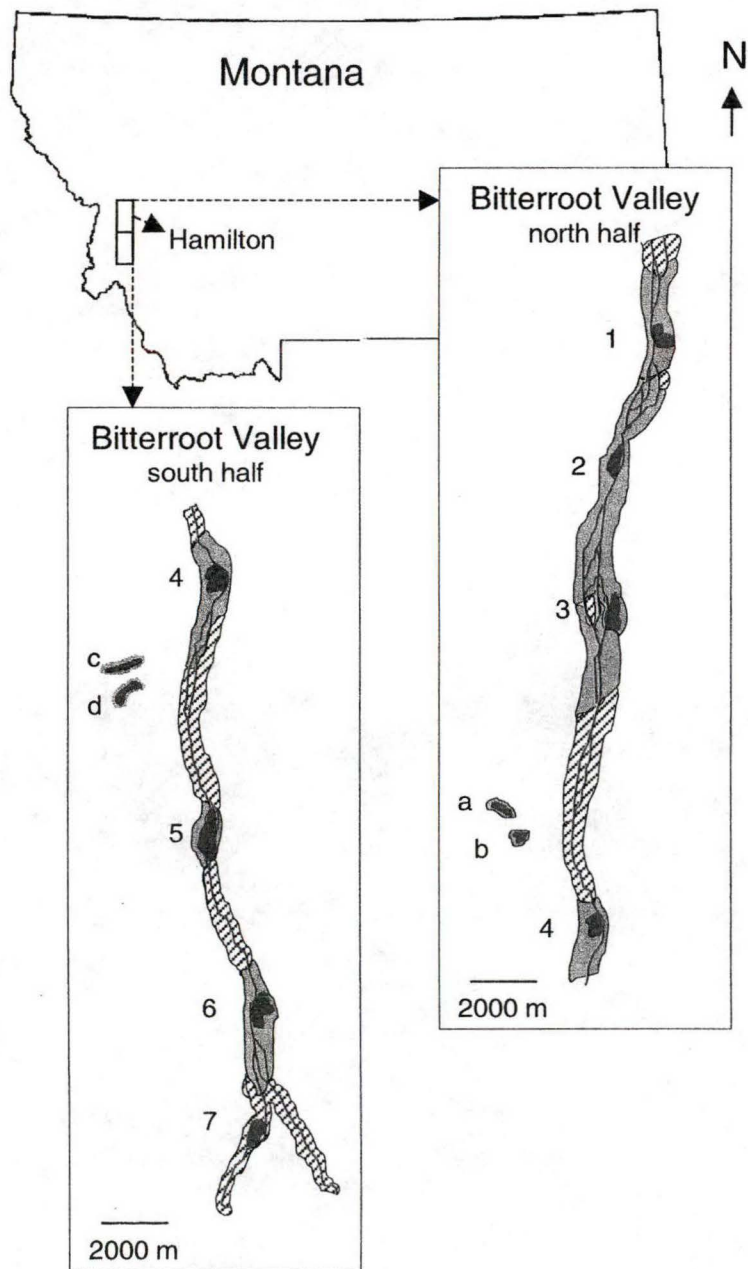
Fig 1. The core sites and expanded search areas within the riparian corridor surrounding the Bitterroot River, Ravalli County, MT. Sites #1 – 7 are the core Bitterroot River sites; sites a – d are the core foothill sites. The core sites were studied 1995-1999; resighting in the expanded search area occurred in 1998-1999.

## RESULTS

*Documenting return and dispersal of marked birds*. – Between 1995-1998, 149 females and 287 males were banded, with 86% of these from the Bitterroot River sites and 14% from the foothill sites. Of these, 44 females and 133 males were resighted at least once in any one or more of the subsequent years. In 1998, the first year of the expanded searches, 17.0% (9 of 47) of the banded birds resighted were found either off the core sites or on a site other than their site of origin, and in 1999 this increased to 29.6% (21 of 71; five of these 21 were also found dispersed off the sites in 1998). Only four of the birds found via the expanded searches were within 0.5 km of their original banding site. Distance moved between years for all resighted birds ranged from 4 – 24,728 meters (for females, median = 153 m; for males, median = 86 m) and was strongly skewed to the right (Fig. 2A and B). Although the linear area searched surrounding and between the core sites was incomplete (Fig.1), the farthest distance that an individual could have dispersed and been detected was approximately 45,000 meters.

*CJS model assumptions and selection*. – Results from the bootstrap GOF tests on the fully parameterized models indicate the estimates adequately fit the data, and no overdispersion adjustments were necessary (core analysis, $\hat{c} = 0.952$; dispersal analysis, $\hat{c} = 0.995$) (White and Burnham1999?). The best approximating model for both the core and dispersal analyses indicated an additive effect of time on survival probability for males and females (Table 1a). Detection probability also differed between sexes with an increasing trend over time (Table1b). Any model with an AIC value within two points of the best model is thought to be a reasonable model given the data (Burnham and Anderson 1998). There were four models for the core analysis and three models for the dispersal analysis with $\Delta$AIC < 2.00 (Table 1A and B), and estimates of $\phi$ and P are slightly different with each model (Appendix 1 and 2). The second best model for both analyses suggested apparent survival varied over time though not between sexes. For the results described below, we report the estimates from the best model ($\Delta$AICc = 0.00); however, the inference would not change substantially with any of the other estimates (Appendix 1 and 2).

*Estimates of apparent survival probability and detection probability*. – Apparent survival probabilities from the dispersal analysis were consistently higher than survival probabilities from the core analysis for both males and females (Table 2 and Fig. 3A and B). The degree of difference depended on year and gender, with $\phi$ being 0.034 (SE = 0.066) – 0.106 (SE = 0.064) higher when the dispersed birds were included. For males, the core analysis mean $\phi$ was 0.418 (SE = 0.034, range 0.346 – 0.490), and for the dispersal analysis mean $\phi$ was 0.493 (SE = 0.037, range 0.410 – 0.588). For females, the core analysis mean $\phi$ was 0.350 (SE = 0.033, range 0.28 – 0.42), and for the dispersal analysis mean $\phi$ was 0.413 (SE = 0.037, range 0.33 – 0.588).

For each year, male detection probabilities were consistently higher than those of females (Table 3), and this held for both analyses. Estimates of detection probabilities in the core analysis were consistently higher than in the dispersal analysis (Table 3). The greatest difference between the two analyses occurred in the first two years of resighting for both sexes; the core $p$'s were 0.06-0.11 higher. For the last two years, $p$ estimates differed by only 0.02 – 0.06.

*Estimates using transient models*. – As expected based on Pradel et al's (1997) finding, the ad hoc test and the residents within the Robson test provided similar estimates of apparent survival

probabilities (Table 2).  For males, the ad hoc $\phi$ were higher than the core analysis $\phi$ for 1996 only; in the Robson test, resident $\phi$s were higher than the core $\phi$ for 1996 and slightly higher for 1998 (Table 4).  The ad hoc $\phi$ estimates were also higher than the dispersal analysis $\phi$ for 1996, but lower in the following years.  In 1997, $\phi$ for the newly marked males was higher (0.02) than the residents.  Based on the Robson test, an estimated 94% of the sampled population males were residents.  For females, survival estimates from the transient models did increase relative to both core and dispersal analysis (Table 4), but the estimates from the transient models varied considerably year to year and had relatively high levels of variation ($\pm$ 0.08 – 0.17 SE).  The Robson test results suggest 54% of females marked are residents.

Fig 2: (A) Distribution of between-year breeding dispersal for adult Yellow Warblers; 1995-1999.
Males (grey) n = 169; females (black) n = 49; range 4-24,728 m.
Distance moved is non-cumulative (e.g. "< 200 is between 100 and 200).
(B) Cumulative distribution functions of dispersal distance for both sexes, showing
the proportion of resighted individuals that were within a given distance of their original banding location.
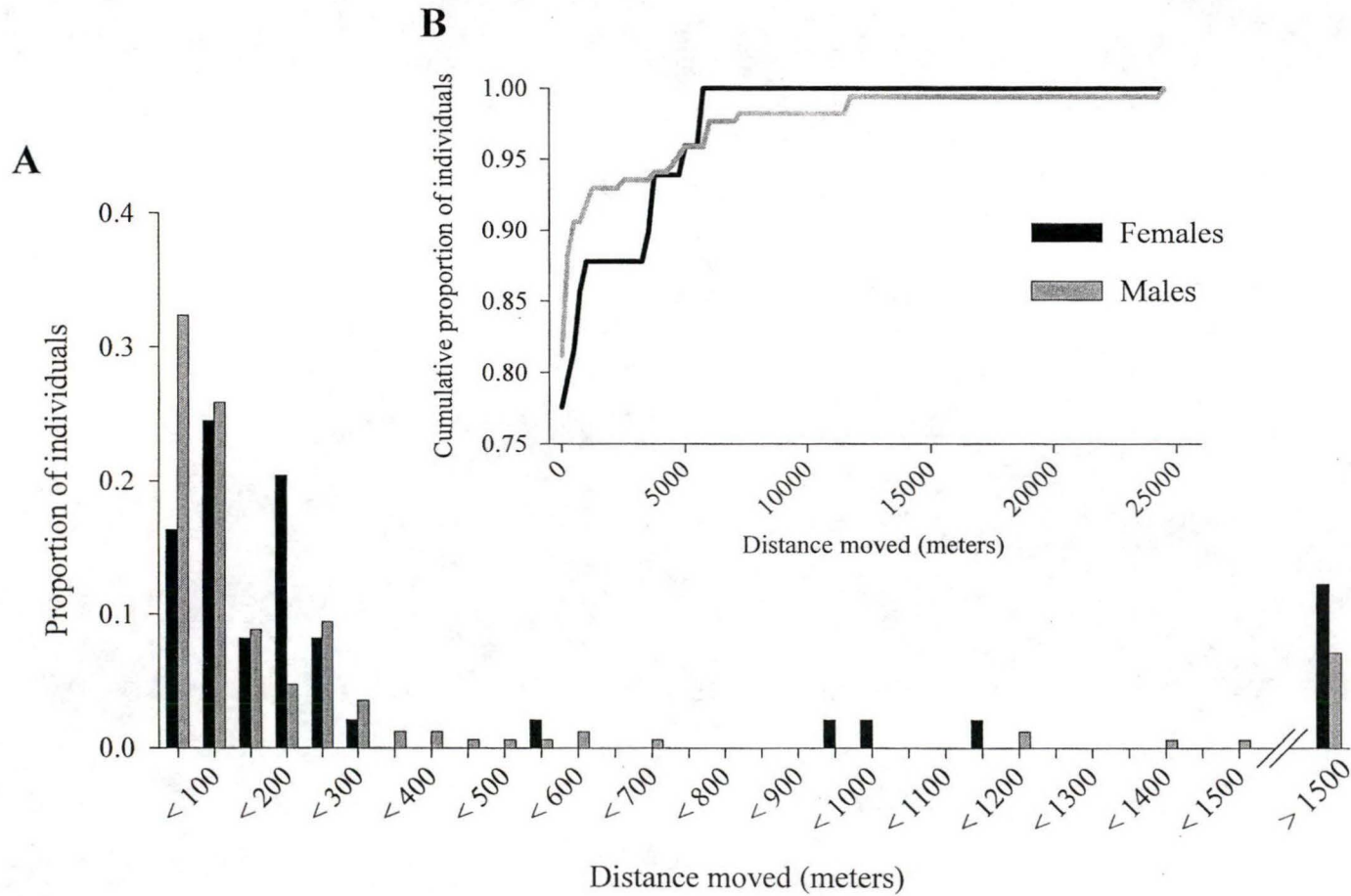
Table 1A and B.  Candidate set of Cormack-Jolly-Seber models used in program MARK ranked by Akaike's Information Criterion (AICc; adjusted for small sample size).

A)  CORE ANALYSIS

| Model [a] | $\Delta$ AICc [b] | AICc weight [c] | np [d] |
|---|---|---|---|
| $\phi(g + t)\, p(g + T)$ | 0.00 | 0.188 | 9 |
| $\phi(t)\, p(g + T)$ | 0.11 | 0.177 | 8 |
| $\phi(g + t)\, p(.)$ | 0.28 | 0.164 | 6 |
| $\phi(g + t)\, p(g)$ | 0.89 | 0.121 | 7 |
| $\phi(g + t)\, p(T)$ | 2.41 | 0.056 | 8 |
| $\phi(t)\, p(g)$ | 2.57 | 0.052 | 6 |
| $\phi(t)\, p(g + t)$ | 2.67 | 0.049 | 10 |
| $\phi(g + t)\, p(g + t)$ | 2.80 | 0.046 | 11 |
| $\phi(t)\, p(.)$ | 4.22 | 0.023 | 5 |
| $\phi(t)\, p(t)$ | 7.78 | 0.004 | 9 |
| $\phi(g * t)\, p(g * t)$ | 12.50 | 0.000 | 18 |
| $\phi(g + T)\, p(g + T)$ | 32.33 | 0.000 | 6 |
| $\phi(g)\, p(.)$ | 50.33 | 0.000 | 3 |
| $\phi(g + T)\, p(g)$ | 60.14 | 0.000 | 5 |

B)  DISPERSAL ANALYSIS

| Model [a] | $\Delta$ AICc [b] | AICc weights [c] | np [d] |
|---|---|---|---|
| $\phi(g + t)\, p(g + T)$ | 0.00 | 0.287 | 9 |
| $\phi(t)\, p(g + T)$ | 1.08 | 0.167 | 8 |
| $\phi(g + t)\, p(g + t)$ | 1.52 | 0.134 | 11 |
| $\phi(t)\, p(g + t)$ | 2.31 | 0.090 | 10 |
| $\phi(g * t)\, p(g * t)$ | 6.10 | 0.014 | 18 |
| $\phi(g + t)\, p(t)$ | 6.19 | 0.013 | 10 |
| $\phi(t)\, p(t)$ | 10.63 | 0.001 | 9 |
| $\phi(g + t)\, p(g)$ | 14.57 | 0.000 | 7 |
| $\phi(g + t)\, p(.)$ | 15.50 | 0.000 | 6 |
| $\phi(t)\, p(g)$ | 17.17 | 0.000 | 6 |
| $\phi(t)\, p(.)$ | 21.59 | 0.000 | 5 |
| $\phi(g + T)\, p(g + T)$ | 43.89 | 0.000 | 6 |
| $\phi(g * T)\, p(g * T)$ | 47.22 | 0.000 | 8 |
| $\phi(g)\, p(g + t)$ | 53.72 | 0.000 | 7 |

[a] Model type.  $\phi$ is apparent survival probability; $p$ is detection probability; g is group (male, female), t is time (year); T is trend in time; (.) is no variation; + is additive effect; * is interaction effect.

[b] Difference in $AIC_c$ values between model.

[c] Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 1998).

[d] Number of estimable parameters.

Table 2.  Adult Yellow Warbler estimates of apparent survival probability (± 1 SE) from the best approximating model for the four different analyses.  Core analysis data include all individuals resighted on their original banding site; dispersal analysis data include all individuals resighted on any of the core sites and within the expanded search areas.

| DATA | 1995 | 1996 | 1997 | 1998 |
|---|---|---|---|---|
| **Core analysis** | | | | |
| males | 0.49 (0.06) | 0.46 (0.05) | 0.35 (0.05) | 0.37 (0.05) |
| females | 0.42 (0.07) | 0.39 (0.06) | 0.28 (0.05) | 0.31 (0.05) |
| | | | | |
| **Dispersal analysis** | | | | |
| males | 0.59 (0.06) | 0.49 (0.05) | 0.41 (0.05) | 0.48 (0.04) |
| females | 0.51 (0.07) | 0.41 (0.06) | 0.33 (0.05) | 0.40 (0.05) |
| | | | | |
| **Transient models** | | | | |
| **Ad hoc test** [a] | | | | |
| males | NA | 0.57 (0.11) | 0.28 (0.06) | 0.38 (0.08) |
| females | NA | 0.64 (0.12) | 0.34 (0.09) | 0.46 (0.10) |
| | | | | |
| **Robson test** [b] | | | | |
| Newly marked | | | | |
| males | 0.50 (0.06) | 0.43 (0.06) | 0.34 (0.08) | 0.39 (0.07) |
| females | 0.30 (0.07) | 0.26 (0.10) | 0.31 (0.10) | 0.22 (0.07) |
| All others | | | | |
| males | NA | 0.50 (0.08) | 0.32 (0.07) | 0.39 (0.09) |
| females | NA | 0.62 (0.17) | 0.33 (0.13) | 0.45 (0.15) |

[a] Using core analysis data, capture history was truncated to include only individuals resighted at least once.

[b] Using core analysis data, $\phi$ for newly marked (one year post banding) were modeled separately from those resighted at least once.

Fig. 3A. Male apparent survival probabilities (1 SE) for Yellow Warblers
in the Bitterroot Valley, MT, 1995-1998.
B. Female apparent survival probabilities (1 SE) for Yellow Warblers
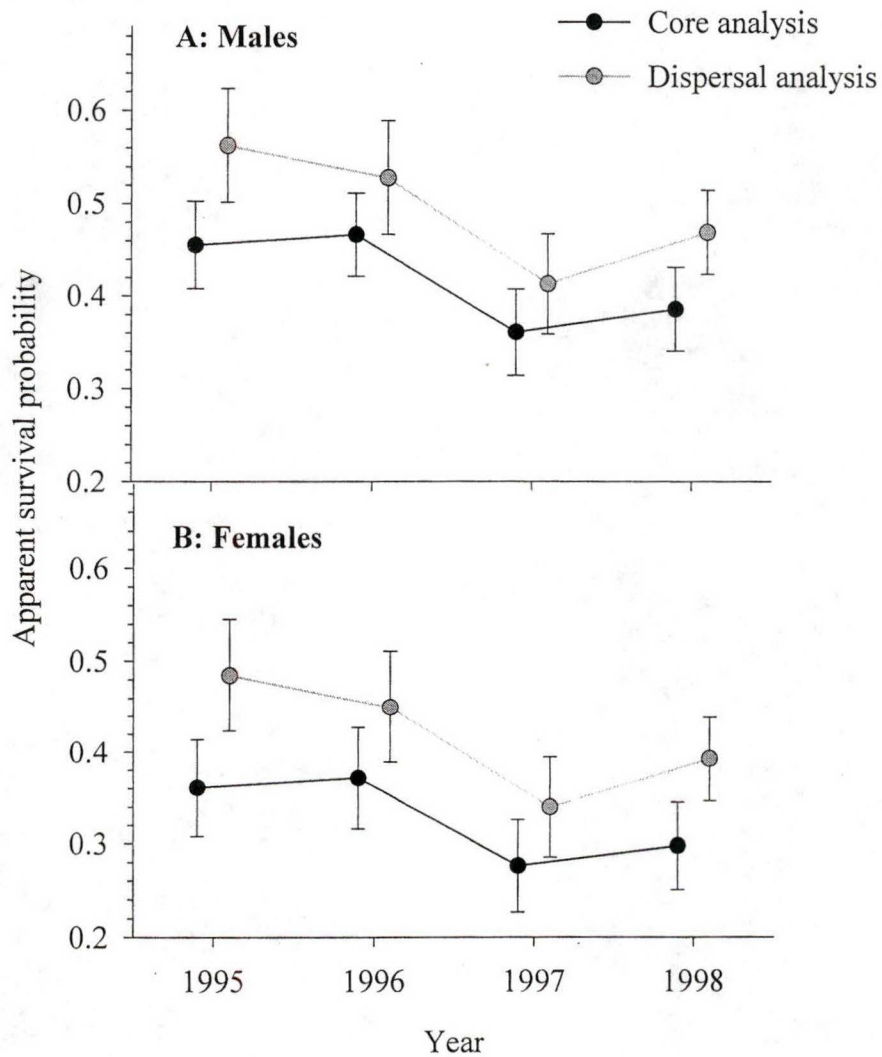in the Bitterroot Valley, MT, 1995-1998.

Table 3.  Adult Yellow Warbler estimates of detection probability ($\pm$ 1 SE) from the best approximating model for the four different analyses.  Core analysis data include all individuals resighted on their original banding site; dispersal analysis data include all individuals resighted on any of the core sites and within the expanded search areas.

| DATA | 1996 | 1997 | 1998 | 1999 |
|---|---|---|---|---|
| **Core analysis** | | | | |
| males | 0.78 (0.07) | 0.84 (0.06) | 0.88 (0.04) | 0.92 (0.04) |
| females | 0.56 (0.12) | 0.65 (0.09) | 0.73 (0.08) | 0.80 (0.08) |
| **Dispersal analysis** | | | | |
| males | 0.69 (0.07) | 0.78 (0.04) | 0.85 (0.03) | 0.90 (0.03) |
| females | 0.45 (0.09) | 0.56 (0.08) | 0.67 (0.07) | 0.77 (0.07) |
| **Transient models** | | | | |
| **Ad hoc test** [a] | | | | |
| males | NA | 0.79 (0.14) | 0.92 (0.06) | 0.97 (0.03) |
| females | NA | 0.57 (0.20) | 0.81 (0.12) | 0.93 (0.08) |
| **Robson test** [b] | | | | |
| males | 0.80 (0.07) | 0.84 (0.04) | 0.88 (0.04) | 0.90 (0.04) |
| females | 0.67 (0.11) | 0.73 (0.08) | 0.78 (0.07) | 0.83 (0.07) |

[a] Using core analysis data, capture history was truncated to include only individuals resighted at least once.

[b] Detection probability modeled as with the core analysis.  *A priori* there was no reason to believe detection probability would differ between the newly marked and those resighted at least once.

Table 4. Differences in estimates of Yellow Warbler apparent survival probability (± 1 SE of the difference) for the transient models relative to the dispersal analysis (from Table 2). "+" indicates the transient estimate was higher than the dispersal estimate; "-" indicates the transient estimate was lower.

| DATA | 1995 | 1996 | 1997 | 1998 |
|---|---|---|---|---|
| **Dispersal analysis** | | | | |
| males | 0.59 (0.06) | 0.49 (0.05) | 0.41 (0.05) | 0.48 (0.04) |
| females | 0.51 (0.07) | 0.41 (0.06) | 0.33 (0.05) | 0.40 (0.05) |
| **Transient models** | | | | |
| **Ad hoc test** [a] | | | | |
| males | NA | + 0.08 (0.12) | - 0.13 (0.08) | - 0.10 (0.09) |
| females | NA | + 0.23 (0.13) | + 0.01 (0.10) | + 0.06 (0.11) |
| **Robson test** [b] | | | | |
| Newly marked | | | | |
| males | - 0.09 (0.08) | - 0.06 (0.08) | - 0.07 (0.09) | - 0.09 (0.08) |
| females | - 0.21 (0.10) | - 0.15 (0.12) | - 0.02 (0.11) | - 0.18 (0.09) |
| All others | | | | |
| males | NA | + 0.01 (0.09) | - 0.09 (0.09) | - 0.09 (0.10) |
| females | NA | + 0.21 (0.18) | 0.00 (0.14) | + 0.05 (0.16) |

[a] Using core analysis data, capture history was truncated to include only individuals resighted at least once.

[b] Using core analysis data, $\phi$ for newly marked (one year post banding) were modeled separately from those resighted at least once.

## DISCUSSION

*Apparent survival probabilities.* – Our analysis indicates that emigration can have substantial effects on estimates of apparent survival probability, $\phi$, for Yellow Warblers. Depending on the year, estimates of $\phi$ increased by 6.5 to 22.9% for males and 5.1 to 29.0% for females when we increased the search area. Our results suggest that researchers must carefully consider the factors affecting apparent survival probability (permanent emigration and mortality) when study areas are small.

Given the potential impacts of permanent emigration on interpretation of apparent survival probability as an estimate of true survival probability, we believe that any attempt to use return rates as an estimate of true survival probability is probably unwise. For example, in 1998 there were 37 female and 52 males banded on the Bitterroot River sites. The return rate in 1999 for these sites combined would have been 0.24 for females. If one had used this as an estimate of survival, it would have been much lower than our estimated apparent survival probability of 0.40; for males the return rate would have been 0.42, compared to an apparent survival probability of 0.48. Differences in return rates for males and females in this study were caused by varying effects of permanent emigration and detection probability, $p$, on these estimates. These results contradict the suggestion by some investigators that movements of migratory songbirds are well understood and that return rates are reasonable substitutes for survival rates (e.g. Mewaldt and King 1985, Villard et al. 1995).

In addition, at least three passerine studies incorporating multiple study areas have shown that the character of the site affected the rates of return. Lawn (1994) color banded Willow Warblers (*Phylloscopus trochilus*) at four adjacent sites of varying habitat quality and found rates of return to the site of banding varied from 14 – 41%. However, he documented breeding dispersal between sites, demonstrating these rates differed because of inconsistencies in site fidelity not survival. Two other studies found differential returns depending on breeding success and quality of site (Black-throated Blue Warbler, *Dendroica caerulescens*, Holms et al. 1996; Bobolink, *Dolichonyx oryzivorus*, Bollinger and Gavin 1989). However, it is important to note that if individuals are highly site faithful, they may return to unsuitable habitat, resulting in a time lag of responses to habitat modifications (Wiens and Rotenberry 1985, Temple and Wiens 1989).

Studies that find differential returns of one or both sexes based on breeding success in the year prior (e.g. Beletsky and Orians 1987, Bollinger and Gavin 1989, Roth and Johnson 1993, Lemon et al. 1996, Haas 1998, Forero et al. 1999; reviewed in Greenwood and Harvey 1982) are widespread in the avian literature, yet most cannot differentiate failure to return from mortality because those birds that were assumed to have dispersed were never located. In this study, four of the six female Yellow Warblers that experienced seasonal nest failure and were located again had dispersed over 2000 m (Cilimburg 2001). Haas (1998) experimentally showed that differences in returns for American Robins (*Turdus migratorius*) and Brown Thrashers (*Toxostoma rufum*) were related to breeding success in the previous season and not reproductive output or quality of the individual.

To our knowledge, this is the first songbird study explicitly designed to use observations of banded songbirds to compare apparent survival probabilities and detection probabilities in an expanded search area to those from a core search area. Others have used mark-recapture with

the Constant Effort Mist Netting scheme (CEMN) and assessed changes in the apparent survival probabilities of songbirds when one study area was expanded to include multiple study areas (Peach et al. 1990, Peach 1993). Peach et al. (1990) captured Reed Warblers (*Acrocephalus scirpaceus*) and Sedge Warblers (*Acrocephalus schoenobaneus*) over 23 years and estimated $\phi$ and $p$ from one sampling area and again when a secondary study area was included. Survival probability was 29% higher for Reed Warblers and 54% higher for Sedge Warblers when both study sites were included. However, their comparison involved two small study sites only 80 m apart. We had a total of 11 study sites, with a 3.5 km minimum distance between the main Bitterroot River sites, though paired foothill sites were as close as 0.5 km (Fig. 1). In a separate study, Peach (1993) compared $\phi$ for five different songbird species from single and multiple study sites and reported that with inclusion of the recaptures from additional study sites, $\phi$ changed from a decrease of 11% to an increase of 128%, depending on the species. However, direct comparisons between CEMN studies and intensive resighting studies such as ours are difficult because CEMN studies are more likely to violate Cormack-Jolly-Seber model assumptions of equal catchability of individuals and geographic closure (resident birds moving in and out of the netting area) (Thompson et al. 1998). In a mark-resight/recapture study, Spendelow et al. (1995) sampled four large breeding colonies of Roseate Terns (*Sterna dougallii*), modeled a movement parameter, and found estimates of apparent survival probabilities increased by 8% as compared to estimates from a single colony previously studied, with this difference attributed entirely to movement and not mortality.

The assumption that adult songbird dispersal is a negligible parameter (e.g., Villard et al. 1995, Pulliam et al. 1992) appears widespread in the literature (Koenig et al. 2000) and is often explicit in modeling attempts such as some spatially explicit population models (e.g. Pulliam et al. 1992). Assumptions regarding lack of dispersal stem from evidence of strong site -fidelity. For example, many studies report that adults commonly return to the same territory as the previous year (e.g. Prairie Warblers (*Dendroica discolor*), Nolan 1978; Willow Warbler (*Phylloscopus trochilus*), Tiainen 1983; Painted Buntings (*Passerina ciris*), Lanyon and Thompson 1986; Indigo Buntings (*Passerina cyanea*), Payne and Payne 1990; Savannah Sparrows (*Passerculus sandwhichensis*), Wheelright and Mauck 1998; White-eyed Vireo (*Vireo griseus*), Hopp et al. 1999). However, as this study shows, site faithfulness by some in a population tells us little about the proportion of birds that may have dispersed.

*Transients.* – We expected estimates from the transient models (ad hoc and Robson tests) to exceed estimates from the dispersal analysis if we did not sample all permanent emigrants in the expanded search or if "transients" that were eliminated from the transient models included individuals other than permanent emigrants. For example, transients eliminated from the analysis may include individuals from the resident population with low survival or recapture probability, especially in systems with extensive heterogeneity. Although results from our analysis (bootstrap GOF) did not indicate extreme heterogeneity, we suspect that differences in estimates of survival probability for dispersal models and transient models in 1996 may have resulted from elimination of "transients" that were not permanent emigrants but resident individuals with low survival. We suspect this, given the similarity between dispersal and transient model estimates in subsequent years, and given the large discrepancy in $\phi$ estimates of newly marked and previously marked birds (see Robson test estimates, Table 4). We acknowledge that we cannot unequivocally conclude that the 1996 transient model estimates are

over-inflated, however, we caution biologists who plan to use these models when study sites are small and the sampling period is short (see below).

Although transient models and dispersal model estimates are reasonably similar ($\Delta\phi = 0.03$) and in the expected direction (transient > dispersal) for survival probabilities in 1997 and 1998, the lower $\phi$ for males in the transient models than the dispersal or core models in these years were not expected. Interestingly, estimates of $\phi$ for newly marked males were higher or equal to estimates for all other birds in 1997 and 1998 (see Robson test estimates, Table 2 and Table 4), and elimination of some of the newly marked birds from the transient models may have caused the observed results.

Such discrepancies and year-to-year variation in the comparisons of survival probabilities among the models results in challenging interpretations. Nonetheless, it does appear that using transient models in the presence of very few to no true transients (permanent emigrants) can lead to misleading results. Inappropriately excluding some newly marked individuals also increased sampling variance (by reducing sample size). Transient models can overestimate the percentage of those not associated with the population, as was likely the case with females in this study (54% transients was highly unlikely because most of these were known breeders). By virtue of this study design we know many individuals are temporary emigrants some years (either not seen one year and then seen again on the study site or in the expanded search area), and because we were banding those breeding on the site, the likelihood that we captured migrants en route is very low. We question whether removing the newly marked cohort would in fact improve the accuracy of survival estimates (as argued by Peach 1993, DeSante et al 1995, Pradel et al. 1997), especially for this type of intensive resighting study.

Peach et al. (1990) ran a CEMN scheme from April to September and considered excluding all early and late season captures but found little evidence those caught in May or August were less likely to be detected in subsequent years. They achieved consistently higher survival estimates by conditioning inclusion on second capture (ad hoc test). However, it remains unclear whether those individuals they excluded were part of the population. They note that that suppressing the first capture resulted in a elimination of a high proportion of recapture data and a corresponding loss of precision. Lawn (1994b) avoided the inclusion of transients by regarding only those singing in same area for at least 5 days as territorial. Some CEMN studies consider as residents those recaptured within-season 7-10 days later (Peach et al. 1991, DeSante 1995, Chase et al. 1997, Gardali et al. 2000). Gardali et al. (2000) also considered any bird recaptured in one or more years to be a resident and noted that the inclusion of all those not recaptured (labeled as transients) would violate assumption of homogeneity of recapture probability.

Instead of relying on transient models, we recommend careful consideration of the timing and method of sampling. Restricting the sampling period to a short period within the breeding season may effectively remove true transients. However, though the population is thought to be reasonably stable during the breeding season, there may be year-to-year variation in migratory schedules (Nichols 1996). Intensive resighting studies benefit from knowledge of territory holding individuals. We found that studies using transient models to adjust $\phi$ were generally CEMN schemes for which it may be more difficult to assess residency because breeding status is unknown. Additionally, a careful definition of "population" is worth consideration; though a

population likely does not include migrants, we argue that "floaters" and other non-breeders should still be considered residents and members of a population.  Again, we urge caution in the use of approaches that may arbitrarily eliminate individuals from the analysis.

*Detection Probabilities.* – For each year, probabilities of detection, $p$, were higher for males than females (Table 3).  Males are more territorially vocal and aggressive, making them easier to resight.  Female Yellow Warblers are less visible during egg laying and incubation, although at other times they will respond to playbacks and allow for resighting of bands.  Detection probabilities for the core analysis were slightly higher than $p$ for the dispersal analysis, because there were more banded birds alive and available to be seen in the expanded search area and the search proficiency was lower.  Additionally, as the search area increased, we found more birds that had not been resighted for at least two years post-marking, negatively affecting the detection probabilities.  Because field workers were consistently resighting on the core sites throughout the season, we believe we found a high percentage of those that held territories within the boundaries of the core sites (possibly as high as 95% of the males and 85% of the females).  Therefore, we suspect that birds that were resighted after being absent for one or more years were more likely to have been temporary emigrants than undetected birds residing within the sites. Studies in which the authors report that because band status of all known pairs was confirmed, detection probability approached 100% are potentially misleading because they do not consider temporary emigration, and we caution researchers not to confidently assume because detection probabilities are high, all marked birds are accounted for.

*Comparative life history.* – Even with our expanded search area, our mean survival probability estimates across all years for Yellow Warblers are still relatively low ($\phi$ for males is 0.49; $\phi$ for females is 0.41).  Roberts (1971) reported Yellow Warbler apparent survival probability estimates of 0.53 ($\pm$ 0.07).  Nichols et al. (1981), using a portion of the data from Roberts (1971) found $\phi$ was 0.62.  The only other mark-resight studies for Yellow Warblers reported a 32.5% return rate for males, but a 90% territory fidelity rate (occupying the same or adjacent territory) among those that did return (Yeserinak and Weatherhead 1997).

These survival probabilities appear to be low relative to other North American migratory songbirds (Table 5).  Nonetheless, comparisons among species can be misleading because the same metric for survival probabilities was not always used, results depend on the shape and size of the study site, and investigations involving small study sites in general did not account for dispersal (Barrowclough 1978).  Although trend analysis from the Breeding Bird Survey does not report declines in Yellow Warbler numbers in Montana (Sauer et al. 1999), our highest $\phi$ combined with the known seasonal fecundity rate for this population (1.47 to 2.02 young/pair/season), results in a population that appears unsustainable (Tewksbury 1999). Tewksbury (1999) suggests such low growth rates are reflective of high rates of parasitism by Brown-headed Cowbirds (*Molothrus ater*).

*Dispersal quantification approaches.* – Two distinct approaches are commonly used to quantify dispersal – mathematical adjustments and field design alterations. Unfortunately, mathematical adjustments lack knowledge of the underlying dispersal distribution and the pattern of long distance dispersal (Koenig et al. 2000), and there is no universal correction factor.  Field designs can be altered by searching for marked birds in either an expanded study area or on secondary

study sites, via radio tracking the movements of individuals, or a combination of these (reviewed in Koenig et al. 2000).  Dispersal information can then be incorporated into various newly developed modeling approaches (reviewed in Nichols 1996 and Nichols and Kaiser 1999).  Our study demonstrates the feasibility of combining multiple sites with expanded searches, especially for species restricted to linear habitats.  Some argue that dispersal studies are necessarily labor intensive and logistically complex (Moore and Dolbeer 1989), but compared to other techniques (radio and/or satellite tagging), resighting is inexpensive requires minimal training.  Advanced technologies allowing satellite and/or radio transmitters attached to 5-10 gram warblers are years away at best (Faaborg et al. 1998, W. Cunningham pers. comm.).

*Conclusions*. – The importance of dispersal information extends beyond issues of survival estimation.  Increasingly, in the face of changing landscapes, demographic investigations attempt to assess the source-sink status of one or more populations.  By definition, source-sink populations are linked by emigration and immigration, yet movement is often not considered explicitly and direct evidence of dispersal is needed (Faaborg et al. 1998).  Landscape structure likely affects movement into and out of habitat patches, and this movement has real consequences regarding persistence in increasingly fragmented landscapes (Faaborg et al. 1998, Walters 1998).

Even though dispersal has received considerable attention in the ornithological literature (see Haas 1995, Brawn and Robinson 1996, Koenig et al. 1996, Clarke et al. 1997, Haas 1998, Ferriere et al. 2000, Koenig et al. 2000, Walters 2000), our understanding is limited.  Koenig et al. (2000) noted that the problem is not simply the lack of unbiased dispersal data, but also the misconception that the frequency of long distance dispersal diminishes to insignificance beyond the boundaries of the study area, allowing investigators to be lulled into believing they have a reasonable understanding of fidelity and dispersal.  We concur with Koenig et al. and hope this study will encourage additional passerine dispersal studies.

According to Clobert and Lebreton (1991), the primary weaknesses in estimating survival probabilities with open population mark-recapture studies are that survival probabilities are underestimated by an unknown factor because of dispersal and that survival probabilities are not necessarily applicable to the entire population, especially if investigators choose highly productive study areas.  Designing investigations with multiple years, multiple study sites and a dispersal component will allow the use of sophisticated modeling and will provide less biased demographic estimations, avoiding the pitfalls of return rates.  Brawn and Robinson (1996) argue that for songbirds, lack of dispersal data is the most prominent missing piece of the songbird demographic puzzle.  Studies of dispersal can help address the discrepancy between monitoring programs and demographic studies.  We support intensive mark-resight studies that offer the best demographic information available.

Table 5. Previously reported model-based apparent survival probability estimates from marked
North American passerine populations.

| Species | $\phi^a$ | sex | study design [b] | citation |
|---|---|---|---|---|
| Acadian Flycatcher | 0.42 | M&F | unk | Nichols et al. 1981 |
| Least Flycatcher | 0.42 | M&F | unk | Nichols et al. 1981 |
| Bell's Vireo | 0.68 ± 0.05 | M | IR | Budnik et al. 2000 |
| Bell's Vireo | 0.47 ± 0.07 | F | IR | Budnik et al. 2000 |
| Red-eyed Vireo | 0.57-0.59 | M&F | IR | Nichols et al. 1981 |
| Warbling Vireo | 0.50 ± 0.05 | M&F | CEMN | Gardali et al. 2000 |
| Barn Swallow | 0.75 | M&F | unk | Nichols et al. 1981 |
| Tufted Titmouse | 0.66 | M&F | unk | Nichols et al. 1981 |
| Tufted Titmouse | 0.54 ± 0.07 | M&F | CEMN | Karr et al. 1990 |
| Carolina Chickadee | 0.60 ± 0.04 | M&F | CEMN | Karr et al. 1990 |
| White-breasted Nuthatch | 0.35 ± 0.01 | M&F | CEMN | Karr et al. 1990 |
| Black-capped Chickadee | 0.62 | M&F | IR | Loery et al.1997 |
| Swainson's Thrush | 0.57 | M&F | unk | Nichols et al. 1981 |
| Wood Thrush | 0.58 ± 0.17 | M&F | IR | Powell et al. 2000 |
| Northern Mockingbird | 0.49 ± 0.11 | M&F | CEMN | Karr et al. 1990 |
| Wilson's Warbler | 0.52 ± 0.04 | M | CEMN | Chase et al. 1997 |
| Wilson's Warbler | 0.45 ± 0.07 | F | CEMN | Chase et al. 1997 |
| Yellow Warbler | 0.62 | M&F | CEMN | Nichols et al. 1981 |
| American Redstart | 0.67 | M&F | unk | Nichols et al. 1981 |
| Northern Cardinal | 0.60 ± 0.06 | M&F | CEMN | Karr et al. 1990 |
| Seaside Sparrow | 0.55 | M&F | unk | Nichols et al. 1981 |
| White-throated Sparrow | 0.61 ± 0.04 | M&F | CEMN | Karr et al. 1990 |
| Dark-eyed Junko | 0.53 ± 0.03 | M&F | CEMN | Karr et al. 1990 |

[a] Apparent survival probability ± 1 SE.
[b] IR is intensive resight study design; CEMN is constant effort mist netting study design; unk is unknown.

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Appendix 1. Adult Yellow Warbler estimates of apparent survival probabilities ($\phi \pm 1$ SE) for models with $\Delta$ AICc < 2.00 (see Table 1a) for both the core and dispersal analyses.

| Model [a] | 1995 | 1996 | 1997 | 1998 |
|---|---|---|---|---|
| **CORE ANALYSIS** [b] | | | | |
| $\phi(g + t)$ $p(g + T)$ $\Delta$AICc = 0.00 | | | | |
|     males | 0.49 (0.06) | 0.46 (0.05) | 0.35 (0.05) | 0.37 (0.05) |
|     females | 0.42 (0.07) | 0.39 (0.06) | 0.28 (0.05) | 0.31 (0.05) |
| $\phi(t)$ $p(g + T)$ $\Delta$AICc = 0.11 | | | | |
|     males | 0.48 (0.06) | 0.44 (0.04) | 0.33 (0.04) | 0.35 (0.04) |
|     females | 0.48 (0.06) | 0.44 (0.04) | 0.33 (0.04) | 0.35 (0.04) |
| $\phi(g + t)$ $p(.)$ $\Delta$AICc = 0.28 | | | | |
|     males | 0.46 (0.05) | 0.47 (0.05) | 0.36 (0.05) | 0.39 (0.05) |
|     females | 0.35 (0.05) | 0.36 (0.05) | 0.27 (0.05) | 0.29 (0.05) |
| $\phi(g + t)$ $p(g)$ $\Delta$AICc = 0.89 | | | | |
|     males | 0.45 (0.05) | 0.47 (0.05) | 0.36 (0.05) | 0.39 (0.05) |
|     females | 0.36 (0.05) | 0.37 (0.06) | 0.28 (0.05) | 0.30 (0.05) |
| | | | | |
| **DISPERSAL ANALYSIS** [c] | | | | |
| $\phi(g + t)$ $p(g + T)$ $\Delta$AICc = 0.00 | | | | |
|     males | 0.59 (0.06) | 0.49 (0.05) | 0.41 (0.05) | 0.48 (0.04) |
|     females | 0.51 (0.07) | 0.41 (0.06) | 0.33 (0.05) | 0.40 (0.05) |
| $\phi(t)$ $p(g + T)$ $\Delta$AICc = 1 08 | | | | |
|     males | 0.57 (0.06) | 0.48 (0.05) | 0.39 (0.04) | 0.45 (0.04) |
|     females | 0.57 (0.06) | 0.48 (0.05) | 0.39 (0.04) | 0.45 (0.04) |
| $\phi(g + t)$ $p(g + t)$ $\Delta$AICc = 1.52 | | | | |
|     males | 0.56 (0.06) | 0.53 (0.06) | 0.41 (0.05) | 0.47 (0.04) |
|     females | 0.48 (0.07) | 0.45 (0.07) | 0.34 (0.06) | 0.39 (0.05) |

[a] Model type (see Table 1 for description of parameters). [or include: $\phi$ is apparent survival probability; $p$ is detection probability; g is group (male, female), t is time (year); T is trend in time; (.) is no variation; + is additive effect; * is interaction effect.]

[b] Core analysis data includes all individuals resighted on their original banding site.

[c] Dispersal analysis data includes all individuals resighted on any of the core sites and within the expanded search areas.

Appendix 2. Adult Yellow Warbler estimates of detection probabilities ($p \pm 1$ SE) for models with $\Delta$ AICc < 2.00 (see Table 1b) ) for both the core and dispersal analyses.

| Model [a] | 1996 | 1997 | 1998 | 1999 |
|---|---|---|---|---|
| **CORE ANALYSIS** [b] | | | | |
| $\phi(g+t)\,p(g+T)$ | | | | |
| males | 0.78 (0.07) | 0.84 (0.04) | 0.88 (0.04) | 0.92 (0.04) |
| females | 0.58 (0.12) | 0.65 (0.09) | 0.73 (0.08) | 0.80 (0.08) |
| $\phi(t)\,p(g+T)$ | | | | |
| males | 0.78 (0.06) | 0.84 (0.04) | 0.89 (0.03) | 0.92 (0.03) |
| females | 0.51 (0.11) | 0.61 (0.08) | 0.70 (0.08) | 0.77 (0.08) |
| $\phi(g+t)\,p(.)$ | | | | |
| males | 0.83 (0.03) | 0.83 (0.03) | 0.83 (0.03) | 0.83 (0.03) |
| females | 0.83 (0.03) | 0.83 (0.03) | 0.83 (0.03) | 0.83 (0.03) |
| $\phi(g+t)\,p(g)$ | | | | |
| males | 0.85 (0.03) | 0.85 (0.03) | 0.85 (0.03) | 0.85 (0.03) |
| females | 0.76 (0.07) | 0.76 (0.07) | 0.76 (0.07) | 0.76 (0.07) |
| **DISPERSAL ANALYSIS** [c] | | | | |
| $\phi(g+t)\,p(g+T)$ | | | | |
| males | 0.69 (0.07) | 0.78 (0.04) | 0.85 (0.03) | 0.90 (0.03) |
| females | 0.45 (0.09) | 0.56 (0.07) | 0.67 (0.07) | 0.77 (0.07) |
| $\phi(t)\,p(g+T)$ | | | | |
| males | 0.69 (0.06) | 0.78 (0.04) | 0.85 (0.03) | 0.91 (0.03) |
| females | 0.41 (0.09) | 0.53 (0.07) | 0.65 (0.07) | 0.75 (0.07) |
| $\phi(g+t)\,p(g+t)$ | | | | |
| males | 0.74 (0.07) | 0.72 (0.07) | 0.79 (0.07) | 0.92 (0.03) |
| females | 0.51 (0.11) | 0.49 (0.11) | 0.59 (0.11) | 0.82 (0.07) |

[a] Model type (see Table 1 for description of parameters).
[b] Core analysis data includes all individuals resighted on their original banding site.
[c] Dispersal analysis data includes all individuals resighted on any of the core sites and within the expanded search areas.